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Study of a narrow hybrid zone between two wolf spiders, *Lycosa ammophila* and *Lycosa ericeticola*, in north Florida (Araneae, Lycosidae)

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Study of a narrow hybrid zone between two wolf spiders, *Lycosa ammophila* and *Lycosa ericeticola*, in north Florida (Araneae, Lycosidae). - The Rosemary Wolf Spider, *Lycosa ericeticola* Wallace, is a member of the *lenta* group of *Lycosa* with a distribution restricted to approximately 3000 hectares. It is parapatric to the widely distributed Sand Loving Wolf Spider, *Lycosa ammophila* Wallace. The genitalia of the males of the two species are dramatically distinct. The two species come into contact in an area of habitat typical for both species and form a narrow hybrid zone of less than 300 meters in width. A morphological study across this overlap zone documents intermediates in male genitalic structure and size dimensions. Behavioral studies demonstrate that the two species readily court and copulate in captivity. Probable historical, ecological and behavioral causes of the speciation of the two species and their subsequent hybridization are discussed.

Key-words: Araneae - Lycosidae - Hybrids - *Lycosa* - Florida - Morphology - Behavior.

INTRODUCTION

Two closely related wolf spiders, the Sand Loving Wolf Spider, *Lycosa ammophila* Wallace, and the Rosemary Wolf Spider, *Lycosa ericeticola* Wallace, have similar habitat preferences but differ in their geographic distributions (Wallace 1942). Both are members of the *Lycosa lenta* group. They inhabit sandhill and high pine habitats (Myers 1990) and are nocturnal hunters in open sandy areas. *L. ammophila* is widespread across northern Florida with a range of more than 5,000,000 hectares whereas *L. ericeticola*, which has been designated a threatened species (Franz 1982), has a highly restricted range of about 3000 hectares, and is restricted to areas with high concentrations of the Florida rosemary, *Ceratiola ericoides*. The distributions of the two species are parapatric (Fig. 1), the western boundary of *L.*

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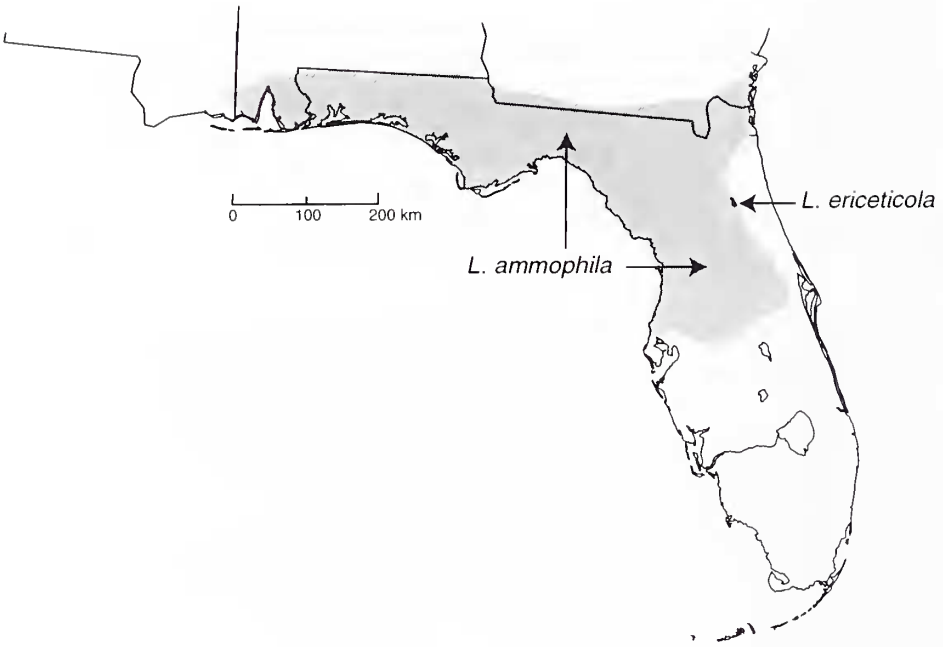


Fig. 1

Distribution map of *Lycosa ammophila* and *L. ericeticola* in Florida (from WALLACE 1942, REISKIND 1987).

ericeticola abutting that of *L. ammophila* (REISKIND 1987). The habitat did not seem to be the limiting factor of its northern and western distribution. Rather, *L. ammophila* replaced *L. ericeticola* in those areas. In one such continuous habitat 6 km west of Interlachen, Florida (Fig. 2) (an area of mostly dirt roads and little development) both species were found together over an east-west distance of about 150 m.

The morphological variation in the male palps of these species is of special interest. Pedipalps of male spiders are used to transfer sperm to the female. They are key taxonomic characters and are diagnostic of specific distinctions in most higher spider groups. Probably the result of sexual selection by female choice (EBERHARD 1985), their detailed and often complex structure are consistent and stable within a species and almost invariably differ from closely related species. This is surely the case in these two species. In *L. ammophila* the median apophysis is straight with a chisel-like posterior medial retrorse tooth (Figs. 3 & 7) whereas in *L. ericeticola* the retrorse tooth is curved with its posterior ending in a distinct downward point (Figs. 4 & 8). A hand lens in the field allows easy discrimination of live specimens. There is no discernible genitalic variation within *L. ericeticola* or in the eastern populations of *L. ammophila* (WALLACE 1942).

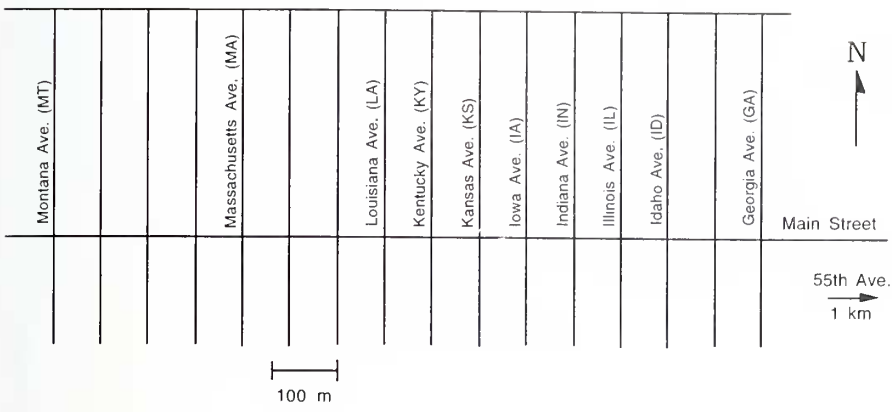


Fig. 2

Map of overlap region between *L. ammophila* and *L. ericeticola*. Collections were made within 100 m of Main Street at the cross streets named.

This paper will examine the two species in their area of overlap to determine if there is evidence for hybridization. Morphology, especially of the male genitalia, supplemented by a study of the effectiveness of their prezygotic isolating mechanisms will be used to test the hypothesis that *L. ericeticola* and *L. ammophila* hybridize.

METHODS

Ninety-five male spiders were collected along a transect crossing the overlap area. The transect was 2.8 km in length and spiders were collected up to 100 meters on either side of a central axis (Main Street in Fig. 2). The most concentrated collections were made in the area of sympatry.

Five measurements were made on each specimen. Three body dimensions: the length of the fourth leg, the carapace length and the carapace width, were made using calipers and are precise to within 0.1 mm. Two genitalic measurements were made by drawing the median apophysis of the male palp (viewed ventrally) using a camera lucida attachment to a Wild stereoscopic dissecting microscope. Measurements of the maximum length of the median apophysis (from the anterior end of its fulcrum to the posterior tip of the retrorse tooth) and its "depth" (see Fig. 5) were made from the drawings and are precise to within 0.001 mm. In addition the "depth"/length (D/L) ratio of the median apophysis was calculated.

All specimens were identified as either *L. ammophila* or *L. ericeticola* on the basis of clear qualitative genitalic features. Those specimens whose designation, based solely on the shape of the median apophysis, were uncertain (Figure 6) were labeled "intermediate" regardless of where they were found in the geographical distribution.

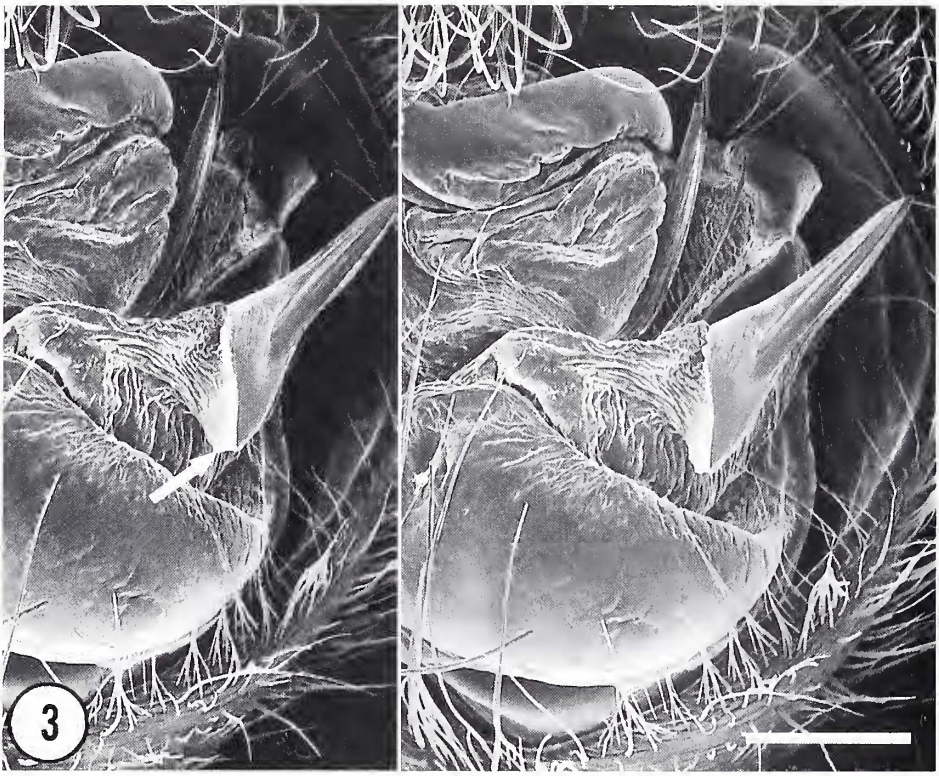


FIG. 3

A stereo ventral view of the left palp of *Lycosa ammophila*. Arrow points to retrorse tooth of the median apophysis. Scale line = 0.4 mm

The five morphological measurements and the D/L ratios allowed statistical comparisons of the two species and their "intermediates." In addition, Neff & Smith (1979) demonstrated the usefulness of a principal component analysis (PCA) in investigating suspected hybrids. The PCA allowed a graphic summary of these data and an independent evaluation of whether the "intermediates" fall between the putative parent species (WILEY 1981).

Adults of both species were tested for compatibility of courtship and copulatory behavior. Test animals were collected from within each species range and at least 1 km from the area of contact. This ensured that the females were of the appropriate identified species. Within and between species encounters were performed in which a male and a female were introduced into a sand filled arena of either 0.5 m x 0.5 m or 0.25 m x 0.5 m and observed for a period of 15 minutes. Efforts were made to use virgin individuals by allowing penultimate specimens to mature in the laboratory. Ten trials of each combination were run. The occurrence of courtship and copulation was noted.

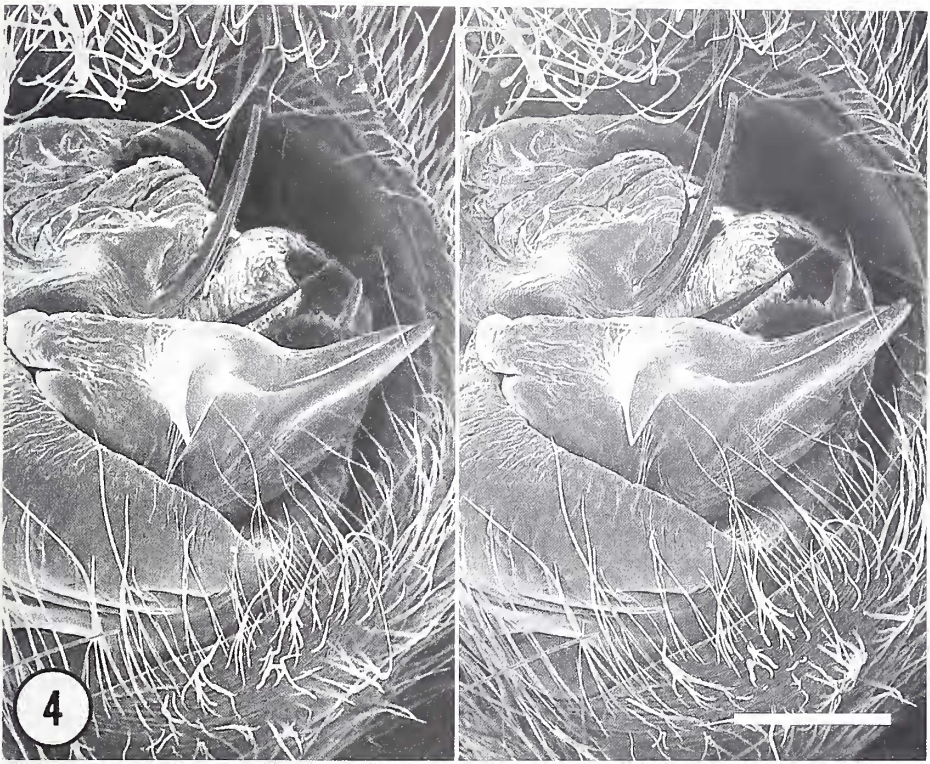


FIG. 4

A stereo ventral view of the left palp of *Lycosa ericeticola*. Scale line = 0.4 mm

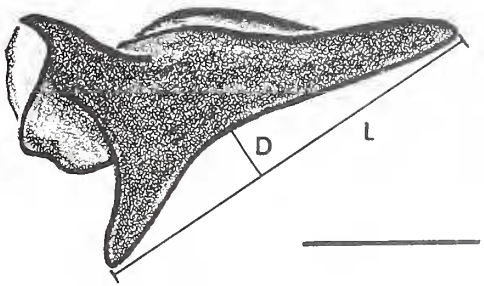


FIG. 5

The dimensions measured on the median apophysis of *Lycosa ericeticola*, L, length, D, depth. Scale line = 0.5 mm

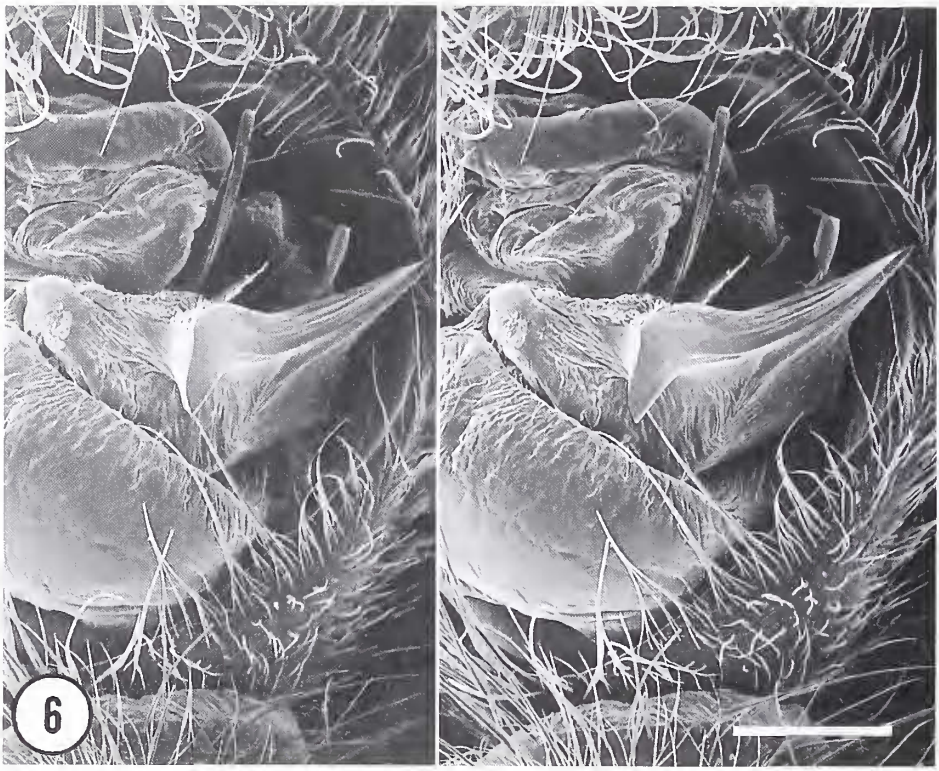


FIG. 6

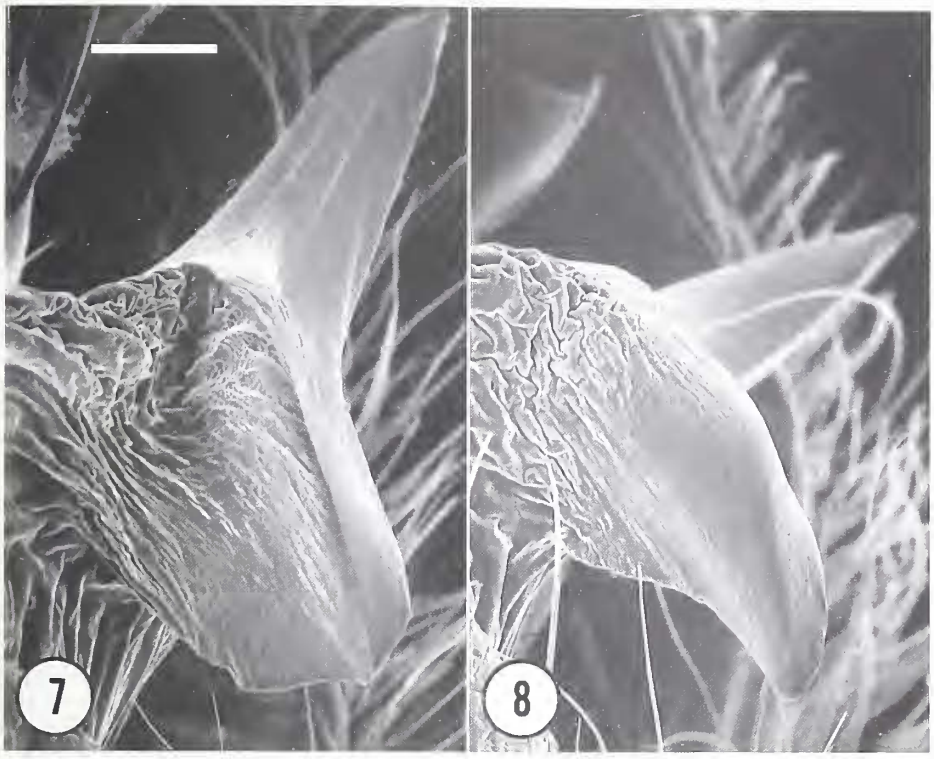
A stereo ventral view of the left palp of an "intermediate" male from Main St. and Kansas Ave. Scale line = 0.4 mm

RESULTS

Morphological intermediates were discovered along the transect in the narrow area where the two species come in contact. They were distributed over a distance of about 280 m, almost twice the width of the area in which both species were found together.

Figures 7-10 illustrate the proximal ends of the median apophyses of *L. ammophila*, *L. ericeticola*, and two "intermediates". The differences between the two species are qualitatively clear and dramatic. The "intermediates" are also distinct, perhaps examples of F_1 progeny.

The PCA allowed the reduction of the six parameters to two principal components accounting for over 87% of the total variance. The first PC (PC1) accounted for 62.8 % of the variance and the second (PC2) for 24.6%. Overall size differences appear to contribute most to PC1, while differences in median apophyses dimensions

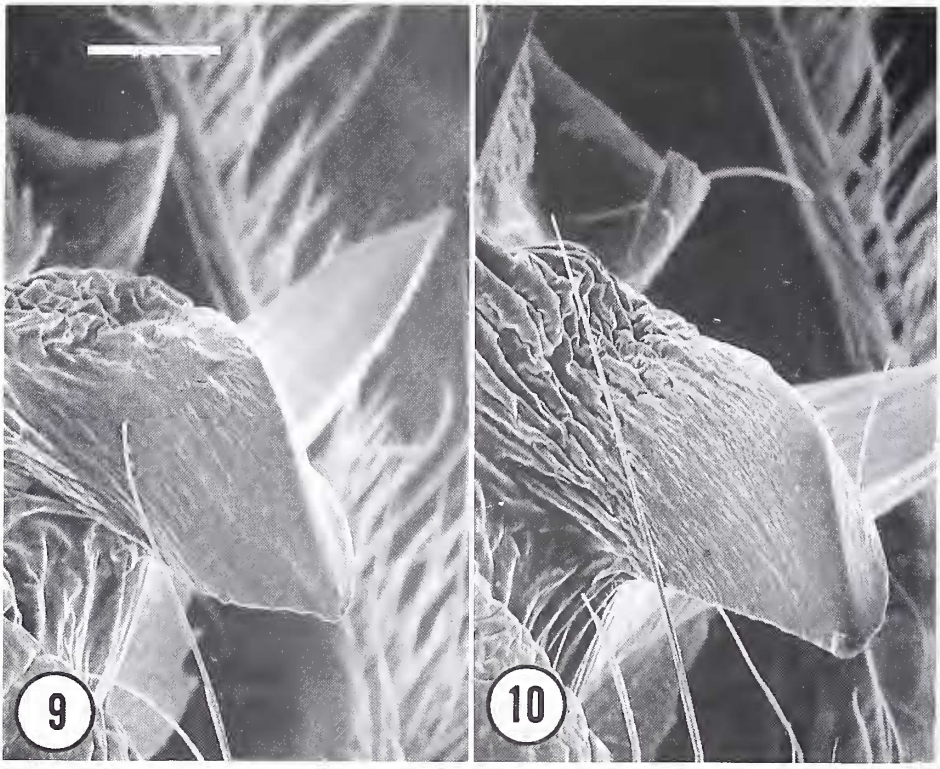


FIGS 7-8

Medial ventral view of the retrorse tooth of the median apophysis. 7. *L. ammophila*. 8. *L. ericeticola*. Scale line = 0.1 mm

primarily contribute to PC2. The resulting graph of these first two components (Fig. 11) allows a visual appreciation of the variation between the individuals of the three identifiable groups. Clearly the "intermediates" all fall between the two established species.

The qualitative differences of the genitalia are well reflected by the D/L ratios (Table 1). In areas where the two species were never caught together the D/L ratios of *L. ericeticola* range from 0.097 to 0.185 while those of *L. ammophila* range from 0.019 to 0.058 ($t=22.25$, $p<0.001$). In the area in which both species have been caught they are still distinct, *L. ericeticola* ranging from 0.084 to 0.179 and *L. ammophila* from 0.029 to 0.070. The "intermediate" genitalia have D/L ratios ranging from 0.055 to 0.111, bridging the gap between the two species. When comparing just those specimens of *L. ericeticola* found in the overlap area with the "intermediates" we found a significant difference in the mean D/L measurements ($t=3.31$, $0.001<p<0.01$). Likewise when comparing the *L. ammophila* specimens found in the overlap region with the "intermediates" ($t=7.38$, $p<0.001$).



FIGS 9-10

Medial ventral views of the retrorse tooth of the median apophysis of two "intermediate" specimens. Scale line = 0.1 mm

The change of D/L ratios along the transect clearly shows the narrow area (about 280 m) in which both species and "intermediates" are found (Fig. 12).

The results of the pairings are recorded in Table 2. The visible expression of male courtship in both species involves the male raising and vibrating his first legs followed by rubbing his first tarsi on the carapace of the female. If the female accepts the advances of the male she will allow him to copulate. A chi-square analysis (df= 2, chi-square= 0.472, $0.5<p<0.9$) indicates no significant difference within and between species with respect to courtship and successful copulatory behavior. From these results there appear to be no well established premating isolating mechanisms between these two species.

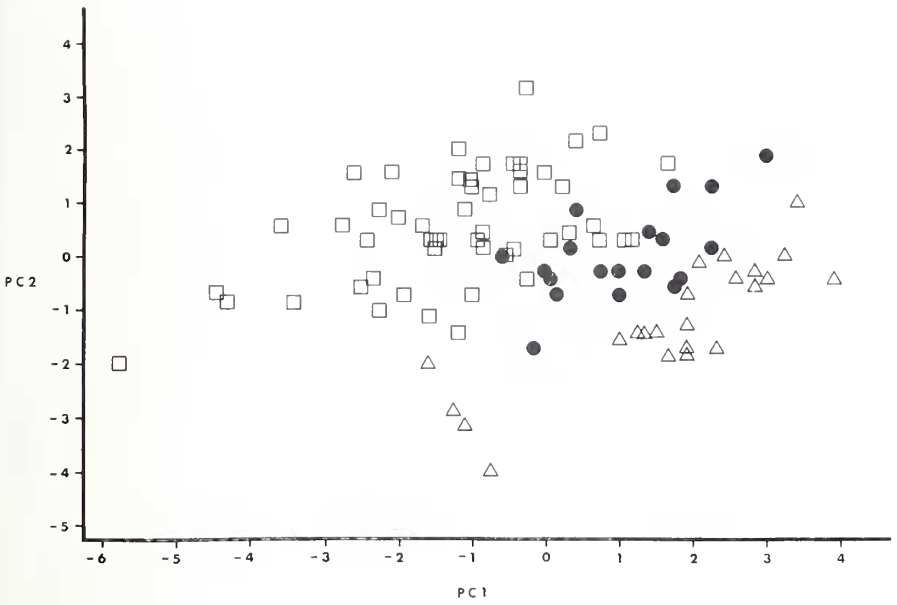


FIG. 11

First and second principal components of the PCA analysis. Open triangles = *L. ammophila*, open squares = *L. ericeticola*, solid circles = "intermediates."

TABLE 1

The D/L ratios of the three forms from different locations along the Main Street transect (see Fig. 2).

		Location										
		MT	MA	LA	KY	KS	IA	IN	IL	ID	GA	55th
L. ammophila	N=	3	6	4	5	6						
	mean:	0.041	0.033	0.041	0.045	0.044						
	max:	0.042	0.058	0.070	0.056	0.069						
	min:	0.039	0.019	0.029	0.033	0.029						
	S.D.:	0.002	0.015	0.020	0.009	0.014						
intermediates	N=			1	2	10	6					
	mean:			0.055	0.064	0.081	0.095					
	max:				0.064	0.104	0.111					
	min:				0.063	0.062	0.066					
	S.D.:				0.001	0.014	0.016					
L. ericeticola	N=				1	7	2	8	9	3	13	9
	mean:				0.102	0.109	0.143	0.127	0.139	0.138	0.151	0.149
	max:					0.142	0.179	0.179	0.185	0.158	0.174	0.171
	min:					0.084	0.107	0.106	0.097	0.119	0.124	0.124
	S.D.:					0.021	0.051	0.022	0.025	0.020	0.014	0.015

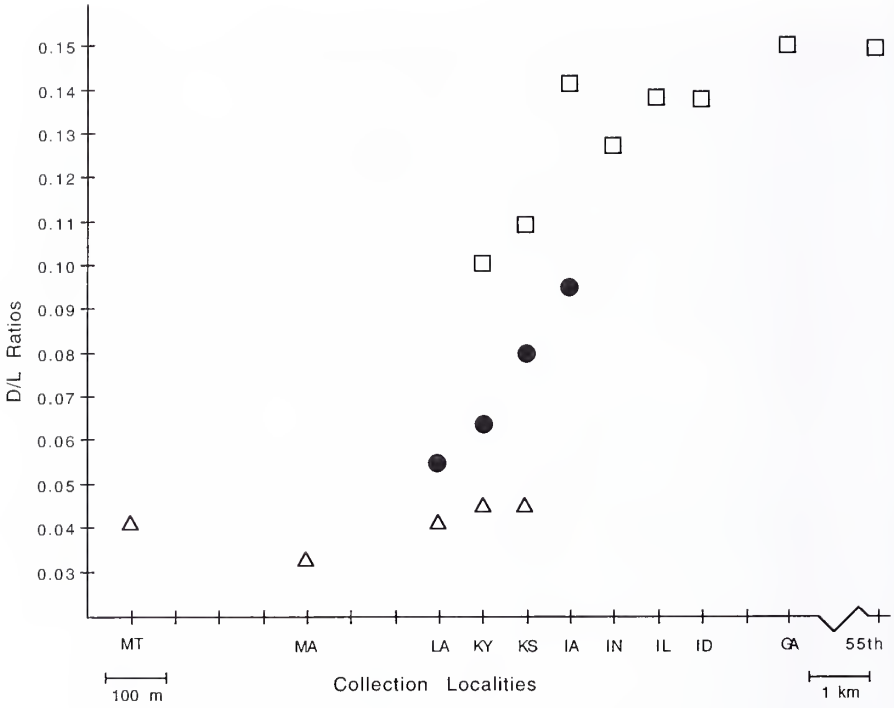


FIG. 12

D/L ratios. Open triangles = *L. ammophila*, open squares = *L. ericeticola*, solid circles = "intermediates." For locality abbreviations see Fig. 2.

TABLE 2

Results of pairing trials between and within the two species. L. ammophila and L. ericeticola

male	female	no male courtship	male courtship no copulation	copulation
L. ammophila	L. ammophila	5	1	4
L. ammophila	L. ericeticola	3	2	5
L. ericeticola	L. ammophila	7	1	2
L. ericeticola	L. ericeticola	3	2	5

DISCUSSION

All the evidence points to the presence of natural hybridization occurring between *L. ammophila* and *L. ericeticola* in an extremely narrow area where their distributions presently overlap. Morphological intermediates are found within and somewhat beyond this area. The statistically significant difference between each puta-

tive parent species and the "intermediates" suggests the production of F^1 hybrids by interbreeding but suggests little if any introgression. While the male genitalic differences between the two species are as distinct as between any pair of lycosid species within the same species group, the pairing experiments demonstrate these differences do not prevent interspecific copulation.

Congeneric lycosids have been hybridized in laboratory experiments to study developmental patterns (Francescoli & Costa 1992) and the inheritance of courtship behavior (Stratton & Uetz 1986). But we know of no reports of natural hybridization in the Lycosidae.

The presence of both species as well as "intermediates" (Fig. 12) in the narrow overlap region makes it unlikely that the variation observed is some sort of steep geographic cline. Rather, it is likely that *L. ericeticola* allopatrically speciated during an early Pleistocene interglacial period when the sea level was significantly higher and small habitat (or real) islands were created along the eastern side of a partly submerged Florida peninsula (Webb 1990, Mayr 1963). Climatic changes or human activities (such as land clearing in the 19th century) may have disturbed natural barriers allowing a relatively recent meeting of the two species. This would explain the apparent absence of effective premating isolating mechanisms between them. Such interspecific coupling would be a necessary, though not sufficient, condition for successful hybridization.

Thus we have a region of secondary intergradation, the result of recent secondary contact between two populations that would be recognized as distinct and separate species by the standard morphological criteria used in spider taxonomic work.

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